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SCIENCE AND ART AMONG THE CHICKENS: PRACTICAL BREEDING IN THE WORK OF RAYMOND PEARL

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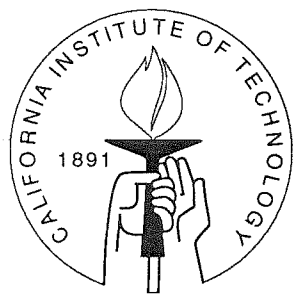

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Science and Art Among the Chickens: Practical Breeding in the Work of Raymond Pearl*

In 1913 Raymond Pearl stood before the American Breeders' Association, his audience composed of scientists, commercial breeders, and hobbyists who were primed to hear a litany of the present and future applications that the science of genetics had developed to aid the art of breeding. As head of biology at the Maine Agricultural Experiment Station, a substation of the federal agricultural research complex, Pearl was ideally placed to comment on the relationship between science and farming. His audience, therefore, expected to hear the typical address given at these gatherings, a speech that praised new scientific knowledge and its advancement of the practical art of agriculture, and that would "so titillate the emotions as to send everybody home uplifted, and, in general, determined to lead a better life." Scientific breeders, Pearl knew, expected him to proclaim that the practical breeder would be able to "soar from [a] scientific foundation to realms of wealth and power." The farmer, in turn, would be encouraged to share, "in a meek and humble spirit of gratitude engendered by the blessings which have been poured at his feet," his practical breeding experience with the scientist. Pearl, however, strayed from this panegyric formula, instead complaining that the ideal picture of the relationship between the scientist and the farmer was "utter banality."[1]

Pearl's caricature of the traditional rhetoric concerning the relationship between scientific theories of inheritance and the practice of breeding stemmed from his frustration with the extreme claims of geneticists, and the negative impact these claims had upon practical breeders. Scientists, believing simply that predictions made years earlier had come true, had not taken the time to evaluate the true contribution that science had made to agriculture. In the first few years of the century, Pearl explained, Mendelian scientists had prophesied that, given the "glittering possibilities" now understood, present animal races could be improved and new and more useful breeds would be created with ease. However, these prophesies had been too optimistic, raising "unwarranted hopes in the minds of

many laymen." These unfulfilled expectations had led to mistrust of scientists, thus hampering not only the availability of financial support for research, but also the actual progress of practical agriculture. In particular, Pearl complained, animal breeders had come to underestimate the importance of Mendelian work for their own practical efforts.[2] Their failure to take advantage of real scientific insights, he argued, was inhibiting breeder efforts to produce improved stock. Pearl's critique of scientific rhetoric was the culmination of six years of research in breeding poultry for increased egg production at the Maine Agricultural Experiment Station in Orono. As an experimental scientist whose job it was to help farmers increase production, Pearl found himself straddling the divide that separated practical and more purely scientific concerns.[3]

Recent work in the history of science and the history of agriculture has sought to understand the relationship between practical breeding concerns and scientific goals of increasing knowledge of genetic processes. For instance, Deborah Fitzgerald, in her work *The Business of Breeding*, evaluated the process by which the "pure science" of plant genetics became the "applied science" of hybrid corn breeding. This interpretation clearly can be applied to Pearl's work with chicken breeding--Pearl obviously attempted to make his conclusions relevant to practical agricultural concerns, and in the end contributed to the formation of the hybrid chicken industry. However, studying Pearl's chicken breeding work demonstrates that the converse process also took place. That is, Pearl chose his theoretical explanations with a view to their ability to address the practical needs of farmers. Reviewing Pearl's work on chicken breeding throughout his tenure at Maine sheds light on the relationship between Mendelism and Wilhelm Johannsen's pure line theory in scientific work during the first two decades of this century. Pearl also provides the historian with a glimpse into the interaction between agricultural industry and the increasingly professional scientific understanding of genetics apart from practical goals in agriculture. In this paper I focus on the role that practical agricultural concerns played in Pearl's evaluation of scientific theory.[4]

Pearl's Journey to Maine

Pearl's interests in chicken breeding were driven by the institutional structure of the scientific research complex that existed in the United States during the late nineteenth and early twentieth centuries. After receiving his Ph.D. from the

University of Michigan in 1902, Pearl remained in Ann Arbor as an Instructor in Zoology until 1905. He studied in Europe during 1905-1906, honing his mathematical ability and his aptitude with biometrical methods, and returned to the United States as an instructor at the University of Pennsylvania. When he returned from abroad, however, Pearl was restless with his teaching duties. His trip to Europe had paid academic dividends, since Karl Pearson asked Pearl to join him as the associate editor of *Biometrika*, but attractive research opportunities were not immediately forthcoming. Wishing to focus his energy on research, Pearl saw no other way to achieve this goal except by going to work at an agricultural experiment station. Offered a research position in 1907, Pearl left his post at Pennsylvania to become the head of the Department of Biology at the Maine Agricultural Experiment Station in Orono.[5]

Since young scientists interested in the problems of inheritance often worked at agricultural posts, Pearl's choice seems quite natural. However, when one considers other factors, Pearl's decision to go to Maine and work on breeding chickens becomes rather mystifying. Chickens seemed an unlikely material for his research, since his previous work had dealt primarily with Planarians and other invertebrates. He also was more interested in understanding developmental processes, and was not particularly intrigued by the goal of understanding the mechanism of hereditary transfer. Explaining this view to his friend and colleague Leon J. Cole, Pearl wrote that he was "becoming convinced that the problems of morphogenesis and growth are the ones which offer most promise of getting somewhere," while "the lines of evolution work now so popular (inheritance, both Galtonian and Mendelian, experimental breeding etc etc.) are likely to lead to just as blind an alley in the end as did pure morphology from the evolution standpoint." For Pearl, understanding factors of inheritance and expecting to understand the process of evolution was akin to learning the chemical constitution of a planet, and expecting to predict its orbit from that information. It was Newton's work "on the laws of morphogenesis of solar systems," he explained, and not abstract chemical knowledge, that had solved the problem of planetary orbits. Complaining that Pearson, William Bateson, Charles Davenport, and William Castle, by emphasizing means of inheritance were "starting at plumb the wrong end of the thing," Pearl suggested that embryologists Hans Driesch and Edwin Conklin were on the right track.[6]

By going to Maine to increase fecundity in chickens, Pearl joined a project that focused on experimental breeding, and so veered from the studies of development that he expected to be most profitable. An ambitious man, Pearl was probably encouraged to go to Maine by his belief that experimental breeding was more accepted in the biological community.[7] In any case, the practical concerns of agricultural breeding did not necessarily entail studying inheritance in "Galtonian or Mendelian" terms, the approach that he disliked most, according to his letter to Cole. Furthermore, Pearl was willing to sacrifice his broader view for a job that would involve no teaching. However, Pearl's belief in the importance of morphogenesis also permeated his experimental work and writing at the Maine Station. Aware of developmental issues and problems, Pearl continually examined physiological and environmental factors along with hereditary explanations.

Upon his arrival at the Maine Station Pearl took up the research on poultry which had been inaugurated by G. M. Gowell about a decade earlier. Throughout the country experiment stations had initiated such research for practical ends, ultimately aiming for the benefit of the farmer and the nation that would be achieved by increasing farm productivity. Originally driven by collectors interested in beautiful and colorful birds, in the late nineteenth century the poultry market became so glutted with breeds that chicken fanciers no longer could subsist on the sale of their animals. Thus the interest of chicken breeders shifted from aesthetics and collecting to egg and poultry production. The growth of this new farming industry attracted the federal agricultural establishment just as the Department of Agriculture, the agricultural colleges, and the agricultural experiment stations were attempting not only to make farming a more scientific pursuit, but also to validate their own existence. The Department of Agriculture reported that in 1899 the value of eggs produced in the country was $144,286,158, and the value of the poultry raised that year was $136,891,877; by 1905 George K. Holmes of the Bureau of Statistics estimated that the value of poultry and eggs had come to equal the value of the nation's wheat crop, amounting to about a half a billion dollars a year. This total had been rising year after year, Holmes claimed, adding that there seemed to be "no limit to the consumption of fresh eggs at a moderate price." This substantial industry thus continued to be a concern of federal, state, and local agricultural organizations which undertook to educate the American farmer on the nature and process of breeding and selling through state fairs, 4-H clubs, and magazines.[8]

By going to Orono, Pearl joined a government supported project that was well underway. During his tenure, which had begun in 1898, Gowell had selected and bred the chickens according to the scientific method of mass selection, also called the German method, in order to increase the number of eggs laid by the individual hens to an average of two hundred eggs per year. Accordingly, he chose the highest laying chickens to be mated with sons of high laying chickens, assuming that by this selection method the egg laying capacity of individuals, and of the flock as a whole, would increase. While practical results had been limited, the work at the Maine Station had been successful in the eyes of the government. In 1904 the program received special funding by the USDA. That same year the station published a bulletin on methods of poultry management that was very well received and increased the station's visibility. Secretary of Agriculture "Tama" James Wilson often held up the program as one of the models of success within the federal research program. In his 1906 report, Wilson asserted that in Maine hens laying 200 eggs a year or more had been found, adding that "the results seem to indicate that by selecting the best layers for breeding purposes and by proper feeding the average egg yield of the flock can be increased."[9] Mass selection in the breeding work at Maine held the key to increasing egg production, he believed.

Gowell's breeding records from 1898-1907, however, did not support Wilson's optimistic attitude, as Pearl discovered soon after his arrival to Orono. When he analyzed the data, Pearl was surprised to learn that after almost a decade of mass selection the egg production of the Maine flock still varied widely, and that the fecundity of the chickens had decreased. One of the foremost experts in biometrical methods in the United States, Pearl used his mathematical talent to evaluate the records of egg production. The analysis proved, he explained, that there was no correlation between the egg production of mothers and the number of eggs laid by their daughters. With no such correlation, selection of high producing hens as the mothers of the next generation clearly would be a fruitless means of attempting to increase the production of a flock. Pearl also was careful to consider developmental factors, making sure that environmental effects had not skewed Gowell's experiments. No such external influences were found. As a result Pearl and his chief assistant Frank Surface reconsidered the usefulness of mass selection in agricultural breeding. They noted that until recently, breeders generally had operated according to the conviction that selection could have a cumulative effect.

Following Darwin, breeders argued that "nature gives successive variations; man adds them up in certain directions useful to him." The Maine station research, however, did not lead to improvement in the flock, bringing the theory of mass selection into question. This conclusion, according to Pearl, was in line with the recent work on pure lines conducted by Wilhelm Johannsen, Hjalmar Nilsson, and his former mentor Herbert Spencer Jennings, which provided "a mass of evidence that the chief if not the entire function of selection in breeding is to *isolate* pure strains from a mixed population."[10]

Pearl realized that this conclusion had significant implications for the results not only of professional breeders employed at the experiment stations, but also for practical farmers struggling to improve their crops, flocks, and herds. Mass selection, widely used by farmers, would not lead to increased productivity. As his data indicated, the external appearance of an individual chicken, or, in this case, its record of production, did not indicate the quality of its progeny. He explained these results in terms of current theory, noting that the Maine results were in accord with "Mendelian work, showing that the constitution of the soma furnishes no certain criterion of the condition or the constitution of the germ cells." Concluding that breeders needed "to do something more than simply breed from high producers," Pearl suggested that the work of Nilsson and Johannsen, as well as that of Hugo deVries, provided "other means" by which to proceed.[11]

From Mass Selection to Isolating Pure Lines

While Mendel explained the difficulties with mass selection, for Pearl the simple differentiation between soma and germ did not suggest a means for improvement. Pure line studies, however, suggested both an explanation for the failure of mass selection, and a procedure for successful breeding. Johannsen had sparked the enthusiasm of the biological community in America with his theory of pure line stability in 1903. Working with beans that were the progeny of one parent continually self-fertilized, Johannsen concluded that within such pure lines selecting continuous variations in order to modify the variety would have no effect; instead, the progeny would exhibit characteristics that represented the mean of the line itself. He applied this theory to large populations by explaining that they were mixtures of pure line populations. Initially, Johannsen's work seemed to support deVries's mutation theory, implying that only evolutionary mutations could

provide the new material for evolution. The pure line theory also raised serious questions about the effectiveness of mass selection as a means to improve the quality of a breeding population.[12] Pearl was probably encouraged to support Johannsen by Jennings, who also came out as a strong advocate of the theory. Jennings tested the theory with *Paramecium*, and concluded that pure lines of these organisms, like Johannsen's beans, regressed to the mean, and could not be selected for hereditary traits.[13]

While their theoretical interpretation was in line with Mendelian assertions, pure line theorists chose to emphasize the constitution of the population rather than that of the individual. Mass selection, according to pure line theory, recombined unalterable qualities from various pure lines. Selection could neither enhance traits nor produce new ones, it could only shuffle and redistribute them. This theory neatly fit the results of Gowell's efforts to increase the fecundity of the chickens at the Maine Experiment Station.[14] Johannsen's theory matched Mendelian understanding in that it claimed that the external qualities of an individual did not indicate what its offspring would be like. However, when compared to Mendelian interpretations, the concept of pure lines also suggested a method for increasing productivity of the flock. By selecting like individuals and breeding them together, thus separating the pure lines that existed within a flock, selection could have a beneficial effect. While traits themselves were not being improved, order was being brought out of the chaos of mixed up lines. The superior lines were purified. Once these high producing lines had been derived from a mixed population, no further selection would be necessary if the stock could be maintained and prevented from cross-fertilizing with other strains. Practical breeders would no longer need to continually select stock to maintain high production.

Thus, while Pearl saw Mendelian evidence in the data from Maine, he emphasized the concept of pure lines in his subsequent chicken breeding experiments.[15] Pearl chose to use the theory of pure lines because he believed it provided a guide to practical farmers in their efforts to improve their own flocks. The theory implied a plan of action--isolate high producing pure lines. A plan of this sort was lacking in Mendelian work. Furthermore, pure line analysis would have appealed to Pearl because it applied more directly to continuous traits, like the trait of egg production.[16] These factors encouraged Pearl to propose that, since the

work of pure line enthusiasts had been limited to plants and invertebrates, he would undertake the "first experimental study of the effect of selection in a higher animal" utilizing his large flock and tracking numerous generations. The "obvious suggestion," he explained, was "to turn to the method of selection which practices the isolation of pure homozygote strains and which has been so successful in the hands of the plant breeders." Pearl theorized that the bloodline, commonly called the strain by breeders, established the limits of performance in egg laying possible by a group of chickens.[17]

Realizing that his work was meant to serve the practical interests of the farming community, before he started his own projects Pearl had thought carefully about just how he should increase egg production. Since prices fluctuated throughout the year, if chickens produced more eggs during certain months, farmers would realize greater profit. Pearl and Surface sought the answer to the question, "which month or months will give [the poultryman] the best estimate of what the total yearly production will probably be for each hen?" They found that hens seemed to have a twelve month laying cycle, with winter production, that is, production from November through February, marking the beginning of the cycle. The chickens exhibited low but increasing production during those months. Spring, from March through May, was the period of highest production, with the subsequent seasons marked by a decline in egg laying. Pearl chose winter production, the season when egg prices were the highest, as his basic measure for overall fecundity, and struggled to increase the winter average per chicken to fifty eggs.[18]

In 1908 Pearl and Surface had implemented an experiment planned by Gowell shortly before his retirement. Gowell intended to determine more exactly the number of eggs laid by the daughters of high producing hens. This experiment also would work to test the theories of deVries and Johannsen, Pearl realized, and would begin to uncover the pure lines within the larger flock. The Maine station thus hatched as many eggs as possible from the hens that laid 200 eggs, and kept exact records of maternal lineage. They did not record the father's pedigree, although they used only the sons of high-producing hens. During the course of the experiment the Maine station members found that usually the high laying offspring were produced by the lower producing hens, while most of the daughters of the high laying hens produced significantly less than 200 eggs. This pattern suggested

that fecundity was inherited in a predictable fashion: high layers produced low producers, while low producers bred high layers. This negative correlation supported the interpretation that selecting the best hens would not increase egg production. However, Pearl noted in a letter to Jennings early in 1909 that there was a strong correlation between sisters in regard to their egg production, which he thought was exactly what should be expected if "the thing goes according to the Nilsson-Johannsen-DeVries schema." Sharing pure line inheritance, sisters would exhibit similar hereditary tendencies, including fecundity.[19]

Next the Pearl and Surface tested the fecundity that resulted when they crossed two established breeds with very different rates of egg production, the high laying Barred Plymouth Rocks and lower producing Cornish Games. The results were striking. When crossing the male of the Rock variety with a Game hen, the progeny were good winter layers. However, when crossing a male Game with a female Rock, the offspring were poor layers. Pearl concluded that "the hybrid pullets whose *mothers* were *good* layers are themselves *poor* layers, while those whose *mothers* were *poor* layers are themselves *good* layers." A hen's egg laying record therefore could not predict the fecundity of her offspring, as Pearl indicated with his rhetorical question: "Could any more striking evidence be adduced to show that the egg record of the mother, in and of itself alone, is a poor indication of what her daughter is likely to lay?" Pearl here emphasized the female's role in producing high layers, perhaps in response to the common practice of selecting hens according to their records of production. However, his tables indicate even more clearly the importance of the male in breeding for good production. The progeny of the Game males all were low producers, following the laying pattern of the male breed. Both the Rock and Game females laid eggs in numbers that would have been expected from the male line.[20]

After ascertaining this pattern of inheritance between two known and apparently pure breeds, Pearl decided to apply Johannsen's theory more directly to his work by isolating the pure lines within his flock. Pearl referred to the "genotype of productiveness (to use Johannsen's very convenient term)" that existed within each pure line. He wanted to discover the separate lines of fecundity, that is, the separate genotypes, that existed among his chickens. Based upon his observation of his own flock, Pearl decided that his chickens were a very heterogeneous group. While he had hens that consistently laid 200 eggs, they varied immensely in their

ability to transmit fecundity to their daughters. Pearl analyzed this result in terms of Johannsen's theory, suggesting that his flock transmitted the genetic egg-laying trait of several different bloodlines. The only way to consistently produce high egg layers was to separate the various lines and breed the highest layers. That approach, however, entailed two problems: first, this method would require close inbreeding, the long term effects of which were still unknown; and second, improving production would require the distinguishing and separating of very confused bloodlines.[21]

In spite of the apparent difficulties, Pearl decided to apply Johannsen's concept of pure lines and genotypes to see if it could help the practical breeder increase fecundity in chickens. Pearl focused on pedigrees and the progeny test. The pedigree, according to Pearl's method, was "the nearest approach which can be made in an organism in which each individual is of one sex only to the *genealogical* unit termed by Johannsen a 'pure line' in self-fertilizing plants." Thus, for Pearl, analyzing animals in terms of pedigree "has underlying it the same considerations which make the 'pure line' so potent an instrument of research in plants and non-sexually reproducing animals." For the purposes of research, the pedigree uncovered the lineage of an animal, locating it within the numerous pure lines that existed in a sexually reproducing population. The pure line theory also suggested that populations tend to be made up of numerous strains and that when mass selection succeeded in altering a population it did so by isolating and thus augmenting the qualities of certain strains within the population. Since offspring do not necessarily follow the appearance of their parents, Pearl argued based on Johannsen, populations typically consist of varying strains and lines, and mass selection merely works to isolate particular characters. Thus Pearl and Surface decided to orient the choice of breeding chicken not around the individual's actual producing ability, but instead on its performance in producing offspring that laid many eggs. Pearl borrowed this concept of progeny testing from plant breeders, and throughout his career emphasized its importance in any successful breeding program.[22]

Sure that his population was very heterogeneous, Pearl suggested that his flock was a mixture of seven lines, A, B, C, D, E, F, and G, each with a different average for egg production. The average for the population as a whole might be 130 eggs annually, he explained, while each individual line ranged from 58 to 197 eggs

per year production. Pearl thus reoriented the study of chickens in Orono around the notion of pure lines as he attempted to isolate the higher and lower producing strains. For the three breeding years, 1908-09, 1909-10, and 1910-11, Pearl successfully separated the higher lines from the lower, with the high producers laying an average of 54 eggs the first winter laying season, 47 the second, and 50 the third, while the low producers laid 22, 25, and 17 eggs, respectively, during the same period. He noted, it "should be understood, of course, that only those pedigree lines are included in the high line averages which uniformly *in each generation* show high fecundity. A similar consideration applies to the low line averages." While Pearl could predict how the better and worse genotypes would produce, he still found the procedure to breed them consistently difficult to master.[23]

In applying this knowledge to practical breeding concerns, Pearl came to realize that the pure line theory, as defined by Johannsen, would be of limited utility to animal breeders. Thus, Pearl stopped short of advocating the pure line theory for practical breeders, concluding that the "fact simply is that a 'pure line' in the strict sense of Johannsen can not by definition exist in an organism reproducing as the domestic fowl does." The genotype concept was useful in analyzing the reproduction of his flock as a whole, but thinking in terms of a large population was very complex. Each flock, Pearl emphasized, would consist of a wide variety of "fecundity genotypes," and in the usual flock "these genotypes will be greatly mixed and intermingled." Furthermore, Pearl asserted that "the range of variation in fecundity *within* the genotype is relatively very large, nearly as great, in fact, as in the general population." He therefore concluded that "while fecundity genotype *means* may be and usually are perfectly distinct, there is much overlapping of individuals in different lines." This problem resulted from the fact that his flock was a sexually reproducing population.[24]

While the genotype concept was for Pearl an accurate theoretical account of the inheritance of fecundity in poultry, the daunting task of separating out the numerous pure lines of fecundity was not, Pearl decided, the best means for the practical chicken farmer to increase egg production. Furthermore, he had come to relate Mendelian theory to Johannsen's pure lines, and realized its the implications for practical breeding. The actual basis for breeding among sexually reproducing animals, he understood, must not be shared pedigree, but rather gametic purity. He explained that it was "only in the sense of a *reproductive* line that we can not, by

definition, have pure lines in organisms where the sexes are separate." By contrast, however, it was "perfectly possible to have a line of such organisms in which all the individuals are *gametically* pure with reference to any particular character." Johannsen had defined pure lines as the progeny of one parent self-fertilized, the reproductive sense referred to by Pearl.[25]

The research and writings of H. Nilsson-Ehle seemed to give Pearl the key for applying Mendel to breeding practice. In 1911 Pearl utilized the multi-factorial theory and research of Nilsson-Ehle to explain the appearance of what originally seemed to be a "mutant" bird appearing among his experimental subjects, noting that it was probably a case of Mendelian segregation. Pearl also must have realized that Nilsson-Ehle's work could be applied to his pure line work. By combining Mendelism with the pure line theory, as Nilsson-Ehle had done, Pearl could explain a continuous range of variation in egg production. Now able to explain continuous variation in Mendelian terms, Pearl realized that the practicality of thinking in terms of pure lines could be magnified by thinking in terms of gametic purity. Not the population as a whole, but the individual birds and their gametic constitution, needed to be the focus of breeding work. Given this understanding, Pearl changed his approach to improving fecundity in chickens in order to better address the methods of practical animal breeders. Believing that understanding the means of trait inheritance would help farmers to understand the effects of inbreeding and crossbreeding, in his subsequent studies Pearl began to consider the underlying Mendelian factors for egg laying that constituted the fecundity of the individual, thus abandoning his hopes of evaluating the strain as a whole.[26]

The Underlying Mendelian Factors that Make up the Genotype

In turning his attention to Mendelian factors, Pearl hypothesized that there were two factors at work in the chickens, one for minimal fecundity, and another for excess production. Pearl explained this as a sex-limited character, where a good male could produce good laying daughters regardless of the quality of the mother. By 1911 these studies had convinced many agricultural scientists that the roosters, rather than the hens, decided the laying ability of chickens. Pearl studied the reproductive apparatus of chickens in order to be sure that levels of egg production were not related to anatomical factors. The results convinced him that hens, regardless of how many eggs they produced, were provided with more oocytes than

could ever be fertilized and mature. Thus Pearl concluded that chickens inherited in greater or lesser degree the physical ability to complete the complex physiological processes that stimulate an egg to develop. With these ideas in mind Pearl decided to rely upon his measures of winter egg production to divide chickens into three groups--those that produced a high number of eggs in the winter, those that produced a low number, and those that produced none at all. Pearl divided high and low producers as those laying more than thirty and those laying less than thirty eggs during the winter. Pearl wanted to test his theory that egg laying followed Mendelian segregation, that the factor for high production probably was inherited through the sire, that it likely was not inherited from the dam to the daughter, and that low fecundity could be inherited either from the sire or dam. Pearl already was convinced that fecundity was a Mendelian trait, noting that his data left "no doubt as to the fact of the Mendelian segregation of fecundity, nor as to the entire distinctness of the things segregated."[27]

In 1912 Pearl delineated a scheme of the factors that could be involved in producing very heavy layers. He proposed three factors: "F" for femaleness, "L1" for basic physiological fecundity, and "L2" for high fecundity. Each factor, L1 or L2 alone, when combined with F, could account for moderate fecundity, but the only the three together, the combination FL1L2, could produce high fecundity, such as that exhibited in high winter production. Hens never formed the gamete FL2, Pearl argued, making it impossible for a hen to pass the trait of high fecundity to her chicks. Thus, high fecundity was a sex-linked characteristic that could be inherited only through a male. Pearl related high fecundity directly to winter production, claiming that an "analysis of extensive statistics has shown that high fecundity represents essentially an addition of two definite seasonal, laying cycles to the basis normal reproduction cycles," the winter and the summer.[28] However, he added that breeds other than his Barred Plymouth Rocks and Cornish Indian Games might have a different sort of gametic scheme as well as different standards of absolute fecundity. From this Pearl continued to conclude that there was no proof that selection could do any more than to isolate pure biotypes or to bring about or perpetuate combinations that otherwise might not have been formed. Certainly there was no proof that a somatic value could be changed or improved.[29]

Hoping that his conclusions might be applicable to practical agriculture, Pearl argued that his scheme was not excessively complicated, and that it could be useful.

While proposing "essentially but two factors," he maintained that other experiments had shown the interaction of two or more factors in the production of a single character, and sex-linked inheritance as well. Pearl had not abandoned the theme of pure lines altogether. Instead he realized that the improvement of a line of animals required "a knowledge of the gametic condition and behavior of the character in which improvement is sought, rather than the somatic." On these grounds Pearl questioned the efficacy of selection, except for isolating pure biotypes from a mixed population, and breeding for a specific combination of characters that might not otherwise arise.[30]

Genetics for the Farmer: Making Mendel Practical

In 1913 Pearl referred to Mendelism as a "dreadful doctrine" in the *Reliable Poultry Journal,* reflecting the relationship between practical breeders and students of heredity. Many farmers were not excited about the assistance that Mendelism might give them in their breeding efforts, and instead believed that the scientific study of breeding was becoming a waste of time and money. As Pearl explained in his speech before the American Breeders' Association that same year, he implicated scientists as much as if not more than the breeders in a lack of communication between the groups. Scientists assumed that their new knowledge inevitably would greatly improve any endeavor to which its knowledge was applicable. Breeding, however, had been practiced for millennia, and so "had attained a relatively high degree of development centuries before any attempt was made to formulate the scientific principles of genetics." Pearl went further, noting that "the practise of the art of animal breeding, so far from languishing, for want of instruction from the science of genetics, is actually immeasurably in advance of that science." Farmers not only had improved breeding without the assistance of science, they also had learned that proper care, environmental conditions, and feeding were crucial to any animal or plant achieving its full hereditary potential. Thus, while genetics had increased the knowledge of the underlying mechanisms that affected the success and failure of breeding, genetics had not been essential to the monumental practical successes breeders had achieved.[31]

What then, Pearl asked "has the rapidly developing science of genetics done for the breeder and what can it do?" Advocating better breeding methods for poultry farmers, Pearl recommended simple improvements, asking that his farmer-

readers choose breeding stock for normal growth and characteristics, that they consider the death of chicks as strong marks against further breeding of the dam, and that they use no birds that had been sick. Pearl reminded breeders to recognize the significance of the male in attempting to increase egg production, rather than relying entirely upon the record of the dam. He also suggested that farmers use the progeny test to be sure that they were achieving the hoped for increase in production.[32] Pearl illustrated the past success of breeders who did not have the benefit of genetic knowledge, noting that the first step in increasing egg production was to begin removing eggs from hen's nests soon after they were laid. This practice had existed long before geneticists had begun their work, and raised annual production significantly, upping the annual average of six to twelve eggs from a wild bird left undisturbed, to fifty to eighty eggs if the eggs were removed regularly. Building on this foundation of practical and widely held knowledge, Pearl explained the ways in which genetics helped breeding results become understandable, and also how genetics could help breeders increase their practical results.[33]

Genetics had contributed to agriculture, according to Pearl, by helping breeders to understand the techniques they already had mastered, and demonstrating to them the ineffectiveness of suspect practices, especially those based upon wives tale. Genetics thus demonstrated the necessity of the progeny test by showing that inherited traits were transferred through "the germinal constitution of the individual rather than in the body or soma." Pearl also emphasized the Mendelian axiom that characters or groups of characters were "inherited as discrete or definite units," and that the law of segregation and recombination explained the various results of inheritance. Reminding practical breeders that "the germinal bases of heritable unit characters can be changed or altered in any respect, only with the greatest difficulty, if at all," Pearl also criticized the traditional conception of Darwinian selection. Maintaining his pure line bias, Pearl continued to argue that selection would not improve traits in any way.[34] Emphasizing the genetic composition of males, Pearl also argued that farmers had to breed using sires that were known to produce high layers. While this was the primary result of his scientific research, Pearl's suggestions went further, advocating traditional approaches that all good farmers and breeders implemented. The other guidelines he offered were to use birds of constitutional vigor, use only high producing females (since only they could produce the proper sort of males), use only males that were

the sons of high-producing females, use a pedigree system to keep track of the birds, early on make numerous matings to see which were the most successful, and finally he suggested inbreeding those who showed the best production.[35] By reiterating what farmers already knew, but including some newer ideas like the progeny test and inbreeding, Pearl hoped to convince the practical breeders that scientific knowledge was relevant to their own practices.

Pearl's emphasis on inbreeding demonstrated his zeal in preaching this scientifically acceptable course to farmers who generally considered inbreeding to be anathema. Originally opposed to inbreeding himself, learning the power of Mendelian inheritance had led Pearl to reconsider--he became something of a missionary about inbreeding. He told farmer breeders that they needed to overcome the fear of inbreeding. "It is a curious paradox of animal husbandry in general," he claimed, "that while, as a matter of fact, every successful breeder of high grade stock practices inbreeding to a greater or lesser extent, a great many of these men are violent, even fanatical, opponents to inbreeding in theory." They called their practice "line-breeding," rather than inbreeding, a distinction "obviously verbal and not biological." Inbreeding was, Pearl explained, the best way to purify one's stock. In fact, he warned about bringing new blood into a flock, since with an ill-advised introduction one could seriously damage years and years of hard breeding work.[36] In an effort to be more relevant to farmers, Pearl attempted to develop quantitative methods that might help breeders. In a paper published that year he proposed a measure of inbreeding, which he called a "coefficient of inbreeding." Inbreeding was important because, as Pearl said, it "reduces the number of different hereditary factors in the stock."[37]

Pearl especially emphasized the value of Mendel to the practical breeder. Mendelian theory had enabled the breeder "to interpret in the light of real knowledge his methods, his successes and his failures." Thinking of egg production and even milk production as unit characters could assist the breeder significantly in improving his flock or herd, he explained. New breeding knowledge also finally refuted breeder traditions that held that environmental conditions, like "contaminations" and "maternal impressions," affected offspring. He concluded with the hope that he had illustrated "that while the results which are being obtained may be of only indirect immediate practical utility, nevertheless they present much which is of fundamental interest to the intelligent breeder of live

stock." He wanted farmers to understand that the "science of genetics is slowly but all the more surely laying a solid foundation of knowledge on which the practical breeder may intelligently revise his practice and interpret his results."[38]

Conclusion:
Practical Results and New Horizons

In the ensuing years Pearl continued to address both farmers and geneticists about the practical and scientific nature of breeding. To the farmers he insisted that they must keep track of the pedigrees of their birds, relying first on the progeny test in their choice of breeders, and remembering that the male played an important role in producing chickens that were high layers.[39] In spite of his efforts to educate farmers about the science of genetics, however, Pearl continued to find that the idea of Mendelian inheritance was under fire from practical breeders. In 1915 he responded to skeptics by comparing his method of breeding to that of mass selection practiced by his predecessor. His results proved that "if one takes a flock of poultry of mixed genetic constitution in respect of fecundity and aims to preserve in his breeding only animals carrying both the factors L1 and L2 necessary for high production, there ought to result a marked and immediate improvement in average flock production no matter what the size of the flock." Pearl had achieved these results by the laying year 1913-14.[40]

Pearl's attempts to encourage farmers to think about Mendelian factors when breeding poultry continually ran up against the issue of selection and its efficacy in breeding chickens for egg production, and in breeding domestic plants and animals in general. Late in 1916 Pearl sought to place current opinion on the importance of selection in evolution in the context of contemporary experimental biology. Delineating the key points of the theory of natural selection, selective elimination and inheritance of surviving traits, Pearl chastised those who he felt were content to accept the theory on logical grounds alone, opting himself for "the 'hard cash' of objective experimental evidence." The biological currency for which Pearl yearned, however, was not easy to come by. Selective elimination seemed proved by some experimenters, disproved by others. Similarly, inheritance of variations could not be demonstrated conclusively. Pearl could rely upon the scientific community when he asserted "that natural selection is no longer generally regarded as the primary, or perhaps even a major, factor in evolution," but practical breeders still

advocated selection as an important means to improving their flocks, herds, and crops.[41]

Ironically, practical breeding concerns eventually led to Pearl's departure from Orono. Although freed from the demands of teaching, upon his arrival to the Maine Station Pearl was pressured to produce practical treatises on topics not related to breeding for farmers. One of the first signs that such demands might become problematic came about around the year 1911 when he was asked to write a treatise on poultry diseases. He complained that this project, about which he had little knowledge or interest, took him four months to complete. By 1916 Pearl realized that his work was under attack--the trustees were complaining that his work was too scientific, and hence not useful enough to the population of Maine. Station critics worried in particular that Pearl was ruining the cattle by cross-breeding them, in Pearl's view missing the point of his work.[42] The trustees had begun to ask for his removal along with that of his ally, station director Charles Woods. Thus in 1918 Pearl left Orono gracefully, heeding President Hoover's call to join the United States Food Administration, organized during the Great War. There he utilized his knowledge and reputation as a poultry expert, as well as his mathematical expertise. When the War ended he joined the faculty of Johns Hopkins University as Professor of Biometry and Vital Statistics.[43]

In spite of his rather unhappy departure from Maine, Pearl's work gained him renown in the community of practical breeders and respect among scientific breeders. Work subsequent to Pearl's further illuminated the nature of fecundity and supported his multi-factorial interpretations of the Mendelian traits involved in its transmission. In 1918, for instance, H. D. Goodale of the Massachusetts Agricultural Experiment Station suggested that fecundity was controlled by a ten different characters, divided into two categories: a) factors that influenced laying at particular points during the year; and b) factors that influenced the intensity of laying during those periods. Later the Hays-Sanborn theory reduced the number of factors involved from ten to five. Historians of the hybrid chicken industry herald Pearl's work as the groundwork for development of the industry. In spite of his frustrations, Pearl uncovered the basic foundation for understanding the nature of fecundity in chickens, and for the applications of that knowledge in practical poultry breeding.[44]

Notes

*I would like to thank Daniel J. Kevles for suggesting that I study Pearl's chicken breeding experiments, for making material in his files from the Pearl papers at the American Philosophical Society available to me, and for his critical comments on this paper. I would also like to thank David A. Valone for his helpful comments and criticism.

[1]Raymond Pearl, "Genetics and Breeding," *Science*, 1913, *37*:539-546, on pp. 539-540.

[2]Pearl, "Genetics and Breeding," pp. 540-541.

[3]For instance, in 1913 in the *Reliable Poultry Journal*, Pearl acted as an apologist for Mendelism, which he called "the proverbial red rag to the bull," as he attempted to calm anti-Mendelian sentiment that existed among practical animal breeders. Pearl argued that his practical breeding hints, constructed for the benefit of the farmer and built on the foundation of several years of practical work at the Maine Agricultural Experiment Station, were not "tainted with this dreadful (?) doctrine." Raymond Pearl, "Breeding for Heavy Egg Production," *Reliable Poultry Journal*, 1913, *20*:812-813 and 860-862.

[4]See Deborah Fitzgerald, *The Business of Breeding: Hybrid Corn in Illinois, 1890-1940* (Ithaca, NY: Cornell University Press, 1990). Barbara Kimmelman undertook a similar task in her dissertation, as she studied the institutional context of various agricultural colleges to further the historians understanding of how genetics emerged as a scientific discipline in the United States. See Barbara Kimmelman, "A Progressive Era Discipline: Genetics at American Agricultural Colleges and Experiment Stations, 1900-1920" (PhD diss., University of Pennsylvania, 1987).

[5]Pearl wrote to his friend Leon Cole in 1906 that he was learning to loath teaching and favored the prospect of going to an agricultural experiment station. See Raymond Pearl to Leon J. Cole, November 15, [1906], Pearl MSS, Leon J. Cole

File, American Philosophical Society. He gave a similar report to William Ritter when Ritter in 1907 offered him a position in La Jolla, California. See Raymond Pearl to William E. Ritter, December 8, 1907, Pearl MSS, William E. Ritter File, American Philosophical Society. Pearl also wrote to A. C. True expressing his interest in Experiment Station work. See also Garland Allen, "Old Wine in New Bottles: From Eugenics to Population Control in the Work of Raymond Pearl," in *The Expansion of American Biology* (New Brunswick: Rutgers University Press, 1991), pp. 233-234; and Sharon E. Kingsland, *Modeling Nature: Episodes in the History of Population Ecology* (Chicago: University of Chicago Press, 1985), p. 56. Charles Rosenberg emphasized that experiment stations often attracted biologists because there formal duties included research and publication. See Charles Rosenberg, *No Other Gods: On Science and American Social Thought* (Baltimore: Johns Hopkins University Press, 1976), p. 168.

[6]Raymond Pearl to L. J. Cole, London, 18 Feb. 1906, Leon J. Cole File, Pearl MSS, American Philosophical Society.

[7]According to L. C. Dunn, however, Pearl's view was within the mainstream of biology of the late nineteenth and early twentieth century. Differentiation and development, Dunn claimed, were the focus of biological investigation rather than the transmission of traits. According to his view, it "was only when some biologists were willing to put aside the intractable problem of development and concentrate on transmission that the problem was analyzed and solved." See L. C. Dunn, *A Short History of Genetics: The Development of Some of the Main Lines of Thought: 1864-1939* (San Francisco: McGraw-Hill, 1965), pp. 47-48.

[8]"Farm Animals and Their Products," *Yearbook of the Department of Agriculture 1901* (Washington DC: Government Printing Office, 1902), p. 783; George K. Holmes, "Causes Affecting Farm Values," *Yearbook of the Department of Agriculture 1905* (Washington DC: Government Printing Office, 1906), 511-532, on p. 512. According to James E. Rice, experiment station scientist in Ithaca, an "industry that amounts annually to half a billion dollars deserves every effort at improvement and the poultry industry is such a one." From James E. Rice, "Report of Committee on Breeding Poultry: Some Principles of Poultry Breeding," *Proceedings of the American Breeders' Association,* 1909, *5*:376-379, on p. 376. See

also Glenn E. Bugos, "Intellectual Property Protection in the American Chicken Breeding Industry," *Business History Review*, 1992, 66:127-168.

[9]David C. Smith, *The Maine Agricultural Experiment Station: A Bountiful Alliance of Science and Husbandry* (Orono, ME: Life Sciences and Agricultural Experiment Station, University of Maine at Orono, 1980), pp. 59-61; James Wilson, "Report of the Secretary," *Yearbook of the Department of Agriculture 1906* (Washington DC: Government Printing Office, 1907), 9-120, on p. 35.

[10]Raymond Pearl and Frank M. Surface, "Is there a Cumulative Effect of Selection? Data from the Study of Fecundity in the Domestic Fowl" *Zeitschrift für Induktive Abstammungs und Vererbungslehre*, 1909, 2:257-275, on p. 258; Raymond Pearl and Frank M. Surface, "Inheritance of Fecundity," Bulletin No. 166 (Orono, ME: Maine Agricultural Experiment Station, March, 1909), 49-84, on pp. 61-73 and 79.

[11]Pearl and Surface, "Is there a Cumulative Effect of Selection," pp. 272-273. Pearl's evaluation of Mendelism, which was positive in spite of his biometrical analysis, exemplifies his willingness to utilize the theoretical potential of both biometry and Mendel. Marga Vicedo and Barbara Kimmelman and have discussed the compatibility of these two theories in the Unites States in "Mendelism and Biometry in Early American Genetics," paper presented at the International Society for the History, Philosophy, and Social Studies of Biology, Brandeis University, July 13-19, 1993. See also Daniel J. Kevles, "Genetics in the United States and Great Britain, 1890-1930: A Review with Speculations," *Isis*, 1980, *71*:441-455.

[12]Nils Roll-Hansen, "The Genotype Theory of Wilhelm Johannsen and its Relation to Plant Breeding and the Study of Evolution," *Centaurus*, 1978, 22:201-235, on p. 205; William B. Provine, *The Origins of Theoretical Population Genetics*, (Chicago: University of Chicago Press, 1971), pp. 94-96; and Frederick B. Churchill, "William Johannsen and the Genotype Concept," *Journal of the History of Biology*, 1974, *7*:5-30.

[13]For example, see Herbert Spencer Jennings, "Experimental Evidence on the Effectiveness of Selection," *American Naturalist*, 1910, *44*:136-145. Provine criticizes Jennings's work and interpretations, as well as the generally positive reception of Johannsen's theory more generally in the American biological community. See

Provine, *Origins of Theoretical Population Genetics*, pp. 97-104. Nils Roll-Hansen and Kyung-Man Kim, however, examine the arguments and find the American response reasonable. See Nils Roll-Hansen, "The Crucial Experiment of Wilhelm Johannsen," *Biology and Philosophy*, 1989, *4*:303-329, on pp. 314-321; and Kyung-Man Kim, "On the Reception of Johannsen's Pure Line Theory: Towards a Sociology of Scientific Validity," *Social Studies of Science*, 1991, *21*:649-679, on p. 664.

[14]Pearl and Surface, "Inheritance of Fecundity," pp. 79-80. Pearl relies upon Hugo deVries for the explanation of Nilsson's work, citing his book *Plant Breeding* (Chicago: Open Court Publishing, 1907).

[15]Kyung-Man Kim has argued that when Pearl understood the failure of mass selection among the chickens, he turned to the pure line theory which was, according to Kim, "the main alternative to Pearson's mass-selection theory." Kyung-Man Kim, *Explaining Scientific Consensus: The Case of Mendelian Genetics* (New York: Guilford Press, 1994), 129. For more on the research programs implied by Mendelism and the pure line theory, see Gerrit A. M. Van Balen, "The Influence of Johannsen's Discoveries on the Constraint-Structure of the Mendelian Research Program. An Example of Conceptual Problem Solving in Evolutionary Theory," *Studies in the History and Philosophy of Science*, 1986, *17*:174-204, especially on pp. 192-199.

[16]Willet M. Hays noted in 1906 that the research and methods of Mendel and deVries were beginning to be implemented in laboratories as well as gardens in order to bring about plant and animal improvement. See *Proceedings of the American Breeders' Association*, 1906, *2*:155-167, on pp. 166-167. For an example see W. J. Spillman, "Application of Mendel's Law to a Practical Problem in Breeding Cattle," *Proceedings of the American Breeders' Association*, 1906, *2*:173-177. However, many biologists believed that many types of inheritance were possible, and these various mechanisms could operate together in the same organism. George Harrison Shull pointed out that there "are many characters that are not unit characters, variations that are not mutations, and inheritance that is non-Mendelian, and such characters, such variations, and such inheritance are also important to the breeder." George Harrison Shull, "Importance of the Mutation

Theory in Practical Breeding," *Proceedings of the American Breeders' Association,* 1907, 3:60-67, on p. 65.

[17]Pearl and Surface, "Is there a Cumulative Effect of Selection?" p. 260; Raymond Pearl, "The Relation of the Results Obtained in Breeding Poultry for Increased Egg Production to Problem of Selection," *Proceedings of the Thirtieth Annual Meeting, the Society for the Promotion of Agricultural Science,* F. W. Rane, ed. (Portland: The Society, 1909), pp. 125-132. Babcock and Clausen agreed in their 1918 textbook, claiming that unquestionably "the greatest possibility for improvement in animal breeding as well as in plant breeding lies in the isolation of recombinations of germinal elements which are better adapted to specific purposes." They included this option along with three other viable methods in plant breeding, including mass selection (the method Pearl had found ineffective in increasing egg production), hybridization, and clonal selection. According to these authors, with the application of Johannsen's genotype conception in analyzing the composition of a field of maize the problem of explaining the rôle of selection in the Illinois corn breeding experiments was immediately simplified." Ernest Brown Babcock and Roy Elwood Clausen, *Genetics in Relation to Agriculture* (New York: McGraw-Hill, 1918), pp. 290-298, 459, and 329.

[18]Raymond Pearl and F. M. Surface, "Poultry Notes--1908," Bulletin 165 (Orono, ME: Maine Agricultural Experiment Station, 1909), pp. 29-48, on pp. 41-46. Pearl and Surface buttressed their assertion about winter laying in another paper published a few years later. See Raymond Pearl and Frank M. Surface, "A Biometrical Study of Egg Production in the Domestic Fowl. II. Seasonal Distribution of Egg Production," Bulletin 110, part 2 (Washington DC: USDA Bureau of Animal Industry, 1911), pp. 81-170, especially on pp. 81-84. See also H. S. Jennings, "Raymond Pearl, 1879-1940," *National Academy of Sciences, Biographical Memoirs,* 1942, 22:296-300. In his 1923 textbook Reginald Crundall Punnett reported that Pearl's use of winter laying as a criteria of overall fecundity was considered sound by Pearl's colleagues. Reginald Crundall Punnett, *Heredity in Poultry* (London: Macmillan, 1923), p. 60.

[19]Raymond Pearl and Frank M. Surface, "Data on the Inheritance of Fecundity Obtained From the Records of the Daughters of '200-Egg Hens,'" Bulletin

166 (Orono, ME: Maine Agricultural Experiment Station, March 1909), pp. 49-51, 82; Raymond Pearl, "Seventeen Years Selection of a Character Showing Sex-Linked Mendelian Inheritance," *American Naturalist*, 1915, *49*:595-608, on p. 596; Pearl and Surface, "Is there a Cumulative Effect of Selection," pp. 257-260; and Pearl to Jennings, Feb. 17, 1909, Pearl MSS, APS, Jennings file.

[20]Raymond Pearl and Frank M. Surface, "Poultry Notes--1909," Bulletin 179 (Orono, ME: Maine Agricultural Experiment Station, 1910), pp. 65-124, on pp. 93-105.

[21]Raymond Pearl, "Inheritance in 'Blood Lines' in Breeding Animals for Performance, With Special Reference to the '200-Egg Hen,'" *Report of the American Breeders' Association*, 1910, *6*:317-326, on p. 320.

[22]Raymond Pearl, "Breeding Poultry for Egg Production," *Maine Agricultural Experiment Station Annual Report for 1911*, Bulletin No. 192 (Orono, ME: Maine Agricultural Experiment Station, 1911), 113-176, on pp. 145-147; and Morley A. Jull, *Poultry Husbandry* (New York: McGraw-Hill, 1930), p. 115. Pearl emphasized his use of the progeny test in "Seventeen Years Selection," pp. 597-598.

[23]Pearl, "Breeding Poultry for Egg Production," pp. 149-150 and 167.

[24]Raymond Pearl, "Inheritance of Fecundity in the Domestic Fowl," *American Naturalist*, 1911, *45*:321-345, on pp. 340-341.

[25]Pearl, "Inheritance of Fecundity in the Domestic Fowl," p. 342.

[26] Pearl, "Inheritance of Fecundity in the Domestic Fowl," pp. 331 and 337. Nils Roll-Hansen discusses Nilsson-Ehle's work in relationship to Mendel and pure lines in "Svalöf and the Origins of Classical Genetics," in *Svalöf 1886-1986: Research and Results in Plant Breeding*, Gosta Olsson, ed. (Stockholm: LTS Fhorlag, 1986), 35-43, on pp. 49-41; and Nils Roll-Hansen, "Le Croisement Des Lignes Pures: De Johannsen a Nilson-Ehle," in *Histoire de la Genetique: Pratiques, Techniques et Thêories*, Jean-Louis Fischer and William H. Schneider, eds. (Paris: ARPEM, 1990), 99-125. Pearl's contemporaries Babcock and Clausen suggested, "were performance and genotypic constitution closely correlated, then this system of mass selection should have been effective. But as a matter of fact the criterion of selection used in

this portion of the investigations, namely total yearly egg production, was evidently not a good index of genotypic constitution, for apparently it failed to distinguish between individuals belonging to a number of intergrading genotypes." Babcock and Clausen, *Genetics in Relation to Agriculture*, pp. 477-499.

[27]According to Pearl "the key to the whole situation is in the fact that the excess production factor, the factor upon which *high* laying records depend, *is never transmitted from a female to her daughters, but only to her sons.*" Pearl, "Address to the New York Farmers," *Proceedings of the New York Farmers, Season 1911-1912*, pp. 37-52, on pp. 44-47; Smith, *Maine Agricultural Experiment Station*, p. 65. Raymond Pearl, "The Mendelian Inheritance of Fecundity in the Domestic Fowl," *American Naturalist*, 1912, *46*:697-711, on pp. 698-702; and Pearl, "The Inheritance of Fecundity," *Popular Science Monthly*, 1912, *81*:364-373 on p. 372.

[28]Pearl, "The Inheritance of Fecundity," p. 367.

[29]Pearl, "The Mendelian Inheritance of Fecundity in the Domestic Fowl," pp. 698-699 and 707-711. In "The Inheritance of Fecundity" Pearl gave the same argument about three factors that might be involved in poultry fecundity. He also related this theory to eugenics, suggesting that perhaps more highly civilized individuals are losing a similar gene for high fecundity. See also Raymond Pearl, "The Mode of Inheritance of Fecundity in the Domestic Fowl," *Journal of Experimental Zoology*, 1912, *13*:153-268, on p. 264. In this paper Pearl gives very specific data on the breeding experiments, tabulating the results for each male and the type of females with which it was mated. The crosses between the Rocks and the Games were the object of Babcock and Clausen's praise in 1918 in their book *Genetics in Relation to Agriculture.* They lauded his work as "something which gives hope for the same definiteness with regard to the problem of the inheritance of fecundity that has been attained in the analysis of the inheritance of other more clearly defined characters." Babcock and Clausen, *Genetics in Relation to Agriculture*, pp. 559-563.

[30]Pearl, "Mendelian Inheritance of Fecundity," pp. 708, 710-711.

[31]Pearl, "Genetics and Breeding," pp. 541-542.

[32]Pearl, "Genetics and Breeding," p. 543; Raymond Pearl, "Breeding for Heavy Egg Production," *Reliable Poultry Journal*, 1913, *20*:812-813 and 860-862.

[33]Raymond Pearl, "Breeding Poultry for Egg Production," *The Farmer's Advocate and Home Magazine* (London, Ontario, William Weld Company, 1866-1951), December 11, 1913, pp. 2160-2161.

[34]Pearl, "Genetics and Breeding," pp. 543-546.

[35]Pearl, "Breeding Poultry for Egg Production," pp. 2160-2161.

[36]Raymond Pearl, "The Fear of Inbreeding," *Farm and Home*, March 13, 1913, pp. 76 and 86. Babcock and Clausen distinguished between line-breeding and inbreeding: "By common agreement the term [line-breeding] does not include inbreeding; it begins with those degrees of relationship which are just outside the pale of inbreeding. It is, therefore, a system of breeding in which cousins of different degrees are mated with each other." This definition probably would not have convinced Pearl that the two were different. Babcock and Clausen, *Genetics in Relationship to Agriculture*, p. 582.

[37]Raymond Pearl, "A Contribution Towards an Analysis of the Problem of Inbreeding," *American Naturalist*, 1913, *47*:577-614.

[38]Raymond Pearl, "Recent Discoveries Which May Modify Breeding Practice," *Breeder's Gazette*, 1913, *64*:1206, 1273, and 1279-1280.

[39]Raymond Pearl, "Improving Egg Production by Breeding," *Maine Agricultural Experiment Station Annual Report for 1914*, Bulletin 231 (Orono, ME: Maine Agricultural Experiment Station, 1914), pp. 217-236, on pp. 225-236.

[40]Raymond Pearl, "Mendelian Inheritance of Fecundity in the Domestic Fowl, and Average Flock Production," *American Naturalist*, 1915, *49*:306-317, on pp. 307-308.

[41]Raymond Pearl, "The Selection Problem," *American Naturalist*, 1917, *51*:65-91, on pp. 66-74. Allen notes Pearl's fall from the Darwinian selection camp in Allen, "Old Wine in New Bottles."

[42]Raymond Pearl to Jacques Loeb, [Rockefeller Institute for Medical Research], September 25, 1916, Pearl MSS, Jacques Loeb File, American Philosophical Society.

[43]Jennings, "Raymond Pearl," pp. 298-299; Raymond Pearl, "Message to the Poultry World From Dr. Raymond Pearl, Biologist and Statistician, Washington D. C.," *Reliable Poultry Journal*, 1918, *25*: 775.

[44]For a summary of Pearl's contribution to poultry breeding along with an explanation of Goodale's work and the Hays-Sanborn theory see Lewis W. Taylor and I. Michael Lerner, "Breeding for Egg Production," Bulletin 626 (Berkeley, CA: California Agricultural Experiment Station, 1938), pp. 5-8; and G. E. Mann, *Poultry Breeding*, Ministry of Agriculture and Fisheries, Bulletin 146 (London: His Majesty's Stationary Office, 1951), pp. 54-56.